DISTRIBUTION AND ECOLOGICAL ADAPTATIONS OF INTERSTITIAL MOLLUSCS IN FIJI

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ABSTRACT

Interstitial molluscs in the Fiji Islands were found in coarse sands associated with coral reefs and beaches. Characteristically the sand was moist, lacked any sulfides and was in an area of constant water exchange. Representative taxa found included species in the class Aplacophora and in the opisthobranch orders Nudibranchia, Philinoglossa and Acochlidiacea. Of these groups, the acochlidiaceans were most numerous in genera represented; the acochlidiacean, *Paraganitus ellynnae* Challis, was the most common species while all others were found in small numbers.

A model for evolution of the marine and freshwater acochlidiaceans in island habitats is presented based on adaptation of interstitial ancestors.

Interstitial molluscs inhabit pore spaces in high-energy, coarse-sand environments. They have been recorded from intertidal and subtidal habitats in both tropical and temperate waters and show remarkable adaptations for their specialized environment (Swedmark, 1968a). Representatives are found in the Aplacophora (subclass Neomeniomorpha) and in the Gastropoda (subclass Opisthobranchia: orders Acochlidiacea, Philinoglossacea and Nudibranchia).

Interstitial solenogasters (Aplacophora) have been described (Marian and Kowalevsky, 1886; Salvini-Plawen, 1968, 1985; Morse, 1979) but up to the present time have not been recorded from South Pacific Islands. Salvini-Plawen (1985), in his description of three new species, referred all solenogasters modified for an interstitial habitat to the family, Meiomeniidae. Acochlidiacean opisthobranchs often are the major component of the molluscan interstitial fauna in coarse sand habitats. These organisms are known from detailed species descriptions, e.g. Bergh (1895), Kowalevsky (1901), Odhner (1937a, b, 1952), Marcus (1953), Marcus and Marcus (1954, 1955) and Swedmark (1968b). Challis (1968, 1970) recorded three species from the South Pacific, *Paraganitis ellynnae* Challis from the Solomon Islands and the new Hebrides and *Pseudunela cornuta* (Challis) and *Maraunibina verrucosa* (Challis) from the Solomon Islands.

Other opisthobranchs adapted for an interstitial environment include interstitial nudibranchs, referred to the genus, *Pseudovermis*. This genus has a worldwide distribution and frequently co-occurs (although in fewer numbers) with the acochlidiaceans. Two species have been described from the South Pacific, *P. mortoni* Challis from the Solomon Islands and *P. hancocki* Challis from New Zealand (Challis, 1969a). The interstitial Philinoglossacea are also represented by one genus, *Philinoglossa* which is found less frequently. However, Challis (1969b) described *P. marcusi*, from the Solomon Islands.

A survey of coarse sand habitats on Viti Levu and adjacent islands in Fiji was conducted in 1978-79 to locate interstitial molluscs. A more systematic study was undertaken at Korolevu beach when it was found to be the richest collecting site. This beach is also the type locality for an interstitial priapulid, *Meiopriapulus fijiensis* Morse (Morse, 1981). Based on the distribution of acochlidiaceans at Korolevu, a hypothesis is proposed for the evolution of interstitial and freshwater acochlidiaceans.

METHODS

Collections were made at localities (Fig. 1) accessible by car and/or boat around the main island of Viti Levu. A transect from high tide to low tide on the beach at Korolevu indicated that interstitial molluscs occurred at approximately the same tide levels in substrata of similar quality and partical size as I had previously observed in other parts of the world. Subsequent areas of sampling were based on this observation. At all localities, sand samples were taken from coarse sand around reefs or from coarse sand beaches that were well-oxygenated, without visible sulfides present in the

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Fig. 1. Map of the Fiji Islands with collecting areas where interstitial molluscs were collected designated by arrows.

sands or fluctuating salinities. Whenever one species of interstitial mollusc was found and if the schedule allowed, more samples were taken from that locality. Cores of sand approximately 10 cm high and 5 cm wide were collected with a garden trowel and individually placed in plastic bags. Subtidal samples were collected in about 1 m of water near the edge of Suva Reef. All samples were transported back to the laboratory of the Institute of Marine Resources at the University of the South Pacific in Suva where living organisms were extracted by elutriation, photographed, studied and fixed in 70% alcohol or Hollande's fixative. Although numerous areas were sampled at any one locality, only those where interstitial molluscs were found are reported.

DESCRIPTION OF COLLECTING SITES

Suva reef is a fringing reef at the outer portion of the delta of the Rewa River. Interstitial molluscs were found there in two habitats. One site was a series of small pockets just inside the algal ridge. These holes were about 0.5 m in depth and often strewn with calcareous sand; they harbored holothurians that break down the chunks of coral into smaller particles. Coarse sand was often banked on the most protected side of the hole. Fine sediments were absent. Water in the holes is continuously exchanged by surge at low tide and the entire area is covered at high tide. The other habitat for interstitial molluscs was along the edge of the channel through the reef. In this passage the surge from wave action is continual and the coarser sand is located along the channel edge. Extensive sampling in the great expanses of sand substratum behind the reef did not yield any interstitial molluscs. This habitat may be unsuitable owing to freshwater intrusion during severe rains. On one occasion, 20 cm of rain was recorded in 24 hr and mud suspended in freshwater runoff from the Rewa River was seen to extend all along the shore side of the reef.

Interstitial molluscs were found in sand from three islands near Viti Levu: Nananu-i-ra off the northeast coast, and Mana Island and the Yasawa Group off the northwest coast. At Nananu-i-ra, coarse sand samples collected from around the bases of dock pilings yielded interstitial molluscs. At all sites the sand was taken from low intertidal regions near the fringing reefs or from subtidal habitats.

Numerous samples were collected at Korolevu, a resort area on the mid-south shore of Viti Levu where a fringing coral reef is located very close to the shoreline (Fig. 2). First suggested as a likely place for interstitial fauna by Professor John Ryland (pers. comm.), the beach is located landward of an inlet in the fringing reef, with a relatively deep offshore channel leading up to the beach. An intermittent stream flows into the inlet from the surrounding hills. Although protected, the area is continually washed by waves and is therefore considered as a high-energy beach.

Fig. 2. Photograph of Korolevu showing the beach where interstitial mollluscs were collected. Note the freshwater stream (S), the deep-water channel (C), the fringing reef (R) and the beach (B). The line represents the position of the transect on the beach.

The most systematic collection of interstitial molluscs was made at Korolevu Beach along a transect established 50 m east of the resort building and extending 15 m from the low tide mark up the beach toward a group of palm trees (Figs. 2, 3). The average slope of the beach was 7°. The sand was a mixture of clastic and coral components with an average phi number of 0.25 and standard deviation of 1.48. There was a sargassum bed just subtidal to the transect. Samples were

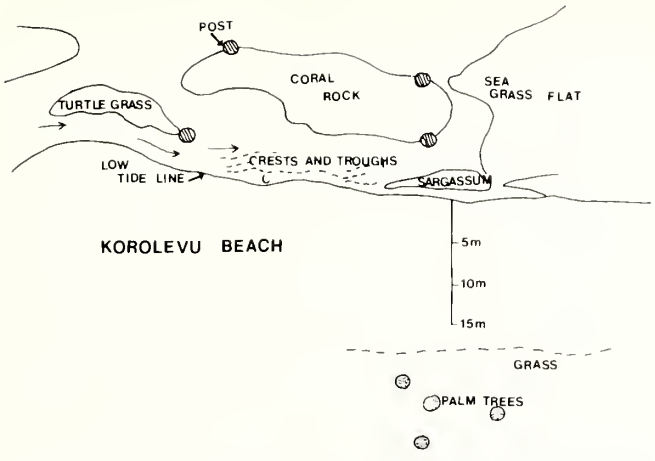

Fig. 3. Diagram of the study area at Korolevu Beach. Cross-hatched circles represent wooden posts and dotted circles represent palm trees.

taken at 1, 2, 3 and 5 m from the low tide line (0.3 m tide) after removal of the dry surface sand. Each sample measured approximately 400-500 cc. Above 5 m, the sand was very dry. Additional samples were taken from a subtidal crest and trough region caused by local currents in an areas to the left of the transect.

SPECIES OF INTERSTITIAL MOLLUSCS COLLECTED

Eight species of meiofaunal Mollusca were found in this study; they are listed in Table 1 and illustrated in figure 4. All except one are Opisthobranchia, with four species in the Acochlidiacea, one in the Philinoglossacea and two in the Nudibranchia. In addition, one species of Aplacophora (subclass Neomeniomorpha) was found at Suva Reef. With the exception of *Paraganitus ellynnae*, the interstitial molluscs were found in small numbers at all habitats examined.

At Korolevu interstitial molluscs were most numerous near the low tide mark at 1 and 2 m (samples I and II, Table 2). These samples were dominated by *Caecum* sp., a minute prosobranch gastropod that feeds on algae. This species also dominated the adjacent subtidal crest and trough region. The acochlidiacean, *Paraganitus ellynnae*, was the most numerous of the four species collected along the transect and the only mollusc found at 5 m. As the sand became dry higher on the beach, samples were taken at increasingly deeper levels. At 5 m from low tide, the wet layer was 12 cm deep; there was a dramatic decrease in numbers of interstitial mollluscs with only a single specimen collected.

In the subtidal crest and trough zone, interstitial molluscs were well represented. Comparing the two areas, the crests were dominated by *Caecum* and more species and individual interstitial molluscs were found in the troughs between the crests. Again, the dominant species was *Paraganitus ellynnae*.

The other opisthobranchs collected at Korolevu included a less common species of acochlidiacean, *Pseudunela* sp., *Pseudovermis* spp. (eyeless and eyed) and *Philinoglossa* sp. Associated interstitial taxa were *Meiopriapulus fijiensis, Saccocirrus* sp., *Protodrilus* sp., *Polygordius* sp., nematodes, turbellarians and copepods.

Among the island collections, the sand beaches of the Yasawa Group had the greatest diversity with three species of acochlidiaceans (Table 2). More systematic collections are needed in these islands.

Table 1. Interstitial molluscs from Viti Levu, Fiji.

Classification	Locality Collected
Class Aplacophora)	
Subclass Neomeniomorpha	
Meiomenia sp.	Suva Reef
Class Gastropoda	
Subclass Opisthobranchia	
Order Acochlidiacea	
Paraganitus ellynnae	Korolevu; Yasawa Island
Pseudunela sp.	Korolevu; Yasawa Island
Hedylopsis sp.	Suva Reef; Yasawa Island
Gastrohedyle sp.	Suva Reef; Nananu-i-ra
Order Philinoglossacea	
Philinoglossa sp.	Korolevu; Mana Island
Order Nudibranchia	
Pseudovermis sp. (eyeless)	Korolevu
P. sp. (eyed)	Korolevu; Suva Reef

DISCUSSION

In Fiji, the dominant group of interstitial molluscs are the acochlidiaceans. Their abundance and position on the beach are similar to those reported by Challis (1969c, d) on the Solomon Islands, but the only species similar in Fiji to those found by Challis was *Paraganitus ellynnae*. This acochlidiacean was also the most abundant species at Korolevu.

In common with the occurrence of interstitial molluscs in other localities (Morse, 1976, 1979), the species collected in Fiji were always associated with sand in areas of continual water exchange and in the absence of sulfides. The sand can be well sorted as was found in the reef pockets on Suva reef or with a mixture of sized particles as shown by the standard deviation from the average phi size from the Korolevu Beach sample.

Distribution of interstitial molluscan genera appears to be cosmopolitan. The occurrence of well known genera in Fiji substantiates this idea. In the Fijian habitats, the acochlidiaceans were of particular interest. They are the only opisthobranchs that are known to have evolved freshwater species and six of the approximately 30 known species of acochlidiaceans are described from freshwater island habitats. In the South Pacific, several species have been found in mountain streams in Indonesia (Bergh, 1895; Bucking, 1933), the Island of Palau (Bayer and Fehlmann, 1960), and the Solomon Islands (Wawra, 1974).

These freshwater species differ from marine species

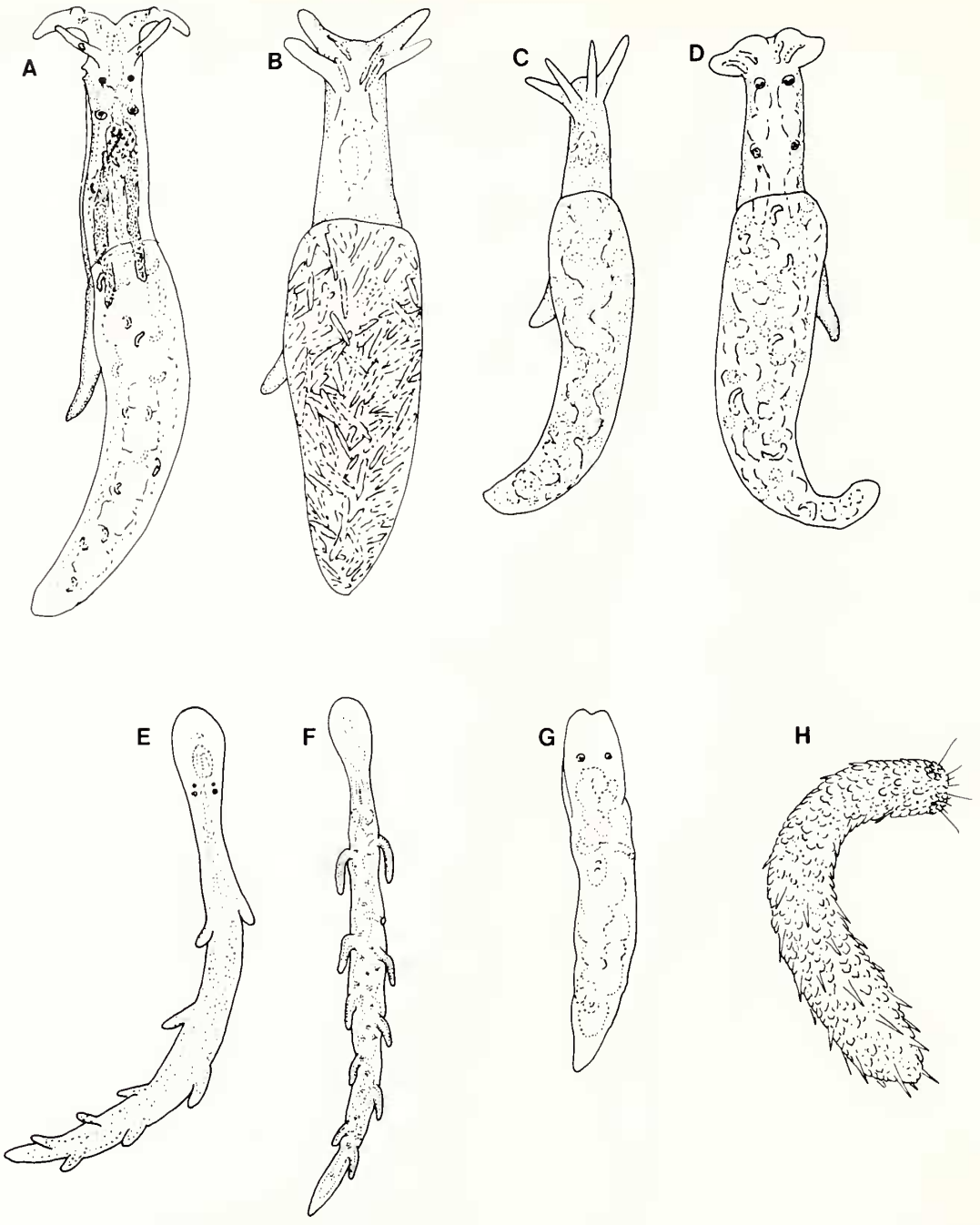

Fig. 4. Drawings of the interstitial molluscs from coarse sand environments on Viti Levu, Fiji: **A.** *Pseudunela* sp. (3.5 mm long); **B.** *Hedylopsis* sp. (1.2 mm long); **C.** *Paraganitus ellynnae* (2.5 mm long); **D.** *Gastrohedyle* sp. (1.2 mm long); **E.** *Pseudovermis* sp. (eyed, 4 mm long); **F.** *Pseudovermis* sp. (eyeless, 3.5 mm long); **G.** *Philinoglossa* sp. (2.3 mm long); **H.** *Meiomenia* sp. (1.3 mm long).

in habitat and size. They live in mountain streams on the underside of rocks and range in size from 3 to 8 mm in length. Those that have been described have a well developed heart-kidney complex and accessory male reproductive structures such as a penis and penis stylet. Professor Starmuhlner (University of Vienna) collected freshwater forms from the undersides of rocks in Fiji (pers. comm.). In my collections in Fiji, four genera of marine interstitial acochlidaceans were found. If the freshwater forms were derived from the interstitial acochlidiaceans, it would be predicted that the ancestral group would have internal structures, that is, accessory reproductive organs and kidney, that were similar. One of the species collected, *Pseudunela* sp., was found to have a well developed heart, a large kidney and a penis with a stylet. Thus

Table 2. Species of interstitial molluscs collected on intertidal transect and subtidal crest and trough zone at Korolevu Beach.

Intertidal - on transect from algal region at edge of low tide to 5 meters.

	Paraganitus ellynnae	*Philinoglossa* sp.	*Pseudovermis* sp.	*Pseudunela* sp.	Environment
Sample I (1 meter)	39	1	0	1	rock and sand, not well-sorted, dominated by *Caecum*
Sample II (2 meters)	74	0	3 (eyeless)	0	well-sorted coarse sand, wet layer 2 cm deep, abundant *Caecum*
Sample III (3 meters)	9	0	1 (eyeless)	0	well-sorted coarse sand, wet layer 5 cm deep
Sample IV (5 meters)	1	0	0	0	well-sorted coarse sand, wet layer 12 cm deep, very dry above

Subtidal - crest and trough zone

	Paraganitus ellynnae	*Philinoglossa* sp.	*Pseudovermis* sp.	*Pseudunela* sp.	Environment
Sample V (crest)	8	1	1 (eyed)	0	coarse shell sand, dominated by *Caecum*
Sample VI (trough)	19	1	1 (eyeless)	1	coarse shell sand, coral chunks

it could be a relic of the stem group that evolved both the stream forms and the other interstitial genera. The other marine interstitial species (*Hedylopsis, Paraganitus,* and *Gastrohedyle*) found in the Fijian sands show regressive evolution toward a vermiform body, a type of evolution first described by Swedmark (1968a). They have a reduced cell number resulting in a simplified reproductive system, a single digestive gland and a reduced or lost heart-kidney system. It would be further predicted that a relic group would be associated with the shores of these islands from which freshwater species have been described. Indeed, Challis (1970) found and described another *Pseudunela, P. coronuta* (Challis), from the Solomon Islands. To test this prediction, more species of marine interstitial acochlidiaceans from island habitats where freshwater species are known should be investigated to see if there are ancestor-like genera present in the interstitial sands.

Climatic conditions that, over time, could have had an impact on such patterns of evolution were witnessed during my tenure in Fiji. They included a hurricane, "Melibe", that changed the topography of Korolevu beach, and floods due to 20 cm of rainfall in 24 hours that impacted the areas behind Suva reef. Freshwater runoffs have created breaks in the fringing reefs, such as is seen at Korolevu, resulting in landward sandy beaches where interstitial molluscs are found. Hurricanes and floods could have been responsible for extensive reassortment of the beach sediments and unsteadiness of habitats that led to further speciation of the acochlidiaceans.

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